A global perspective of ground level, 'ambient' carbon dioxide for assessing the response of plants to atmospheric CO_2

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Abstract

For most studies involving the response of plants to future concentrations of atmospheric carbon dioxide (CO_2), a current concentration of 360–370 μatm is assumed, based on recent data obtained from the Mauna Loa observatory. In the present study, average seasonal diurnal values of ambient CO_2 obtained at ground level from three global locations (Australia, Japan and the USA) indicated that the average CO_2 (at canopy height) can vary from over 500 μatm at night to 350 μatm during the day with average 24-h values ranging from 390 to 465 μatm. At all sites sampled, ambient CO_2 rose to a maximum value during the pre-dawn period (03.00–06.00 hours); at sunrise, CO_2 remained elevated for several hours before declining to a steady-state concentration between 350 and 400 μatm by mid-morning (08.00–10.00 hours). Responses of plant growth to simulations of the observed variation of *in situ* CO_2 were compared to growth at a constant CO_2 concentration in controlled environment chambers. Three diurnal patterns were used (constant 370 μatm CO_2, constant 370 during the day (07.00–19.00 hours), high CO_2 (500 μatm) at night; or, high CO_2 (500 μatm) at night and during the early morning (07.00–09.00 hours) decreasing to 370 μatm by 10.00 hours). Three plant species – soybean (Glycine max, L (Merr.), velvetleaf (Abutilon theophrasti L.) and tomato (Lycopersicon esculentum L.) – were grown in each of these environments. For soybean, high night-time CO_2 resulted in a significant increase in net assimilation rate (NAR), plant growth, leaf area and biomass relative to a constant ambient value of CO_2 by 29 days after sowing. Significant increases in NAR for all three species, and significant increases in leaf area, growth and total biomass for two of the three C3 species tested (velvetleaf and soybean) were also observed after 29 days post sowing for the high night/early morning diurnal pattern of CO_2. Data from these experiments suggest that the ambient CO_2 concentration experienced by some plants is higher than the Mauna Loa average, and that growth of some agricultural species at *in situ* CO_2 levels can differ significantly from the constant CO_2 value used as a control in many CO_2 experiments. This suggests that a reassessment of control conditions used to quantify the response of plants to future, elevated CO_2 may be required.

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Introduction

Based on modern records of CO_2 data obtained from the Mauna Loa observatory, atmospheric CO_2 concentration has risen from 315 µatm in the late 1950s to ≈ 370 µatm today (Keeling & Whorf 1994). The Mauna Loa data represent the longest continuous direct record of measured atmospheric CO_2 for the 20th century. As the global demand for energy and agricultural land increases, deforestation and fossil fuel burning will continue to be anthropogenic sources of atmospheric CO_2. It is anticipated that atmospheric CO_2 should reach anywhere from 600 to 1000 µatm by the end of the 21st century (Houghton *et al.* 1996).

With respect to plant biology, it is clear that the ongoing increase in atmospheric CO_2 can affect plant function, principally through its direct effects on photosynthesis, photorespiration, dark respiration and stomatal physiology. Recent surveys of the literature indicate hundreds of experiments which show that as CO_2 increases, substantial increases in photosynthesis, growth and yield can occur (Kimball *et al.* 1993; Poorter 1993; Curtis & Wang 1998; Wand *et al.* 1999). In the majority of these studies, fixed concentrations of CO_2 given 24 h per day are used as the control, where the fixed concentration is based on recent CO_2 measurements from the Mauna Loa observatory which are usually in the range 330–360 µatm.

However, does the concentration at field sites accurately reflect the Mauna Loa standard? Potential differences in ground-level CO_2 can occur as a result of ground level respiration or wind speed (Allen 1971; Verma & Rosenberg 1976; see also Brown & Rosenberg 1970 for diurnal variation at 1225 m in an isolated prairie site). If differences between the observed and expected concentrations of ambient CO_2 exist, are these differences sufficient to alter plant growth? If so, then our definition of what constitutes ambient CO_2 for experimental purposes deserves additional scrutiny.

In the current study the average ambient CO_2 concentrations were examined from four global field sites. The objectives were twofold: (i) to test the assumption that ambient CO_2 data in the field accurately reflects global atmospheric CO_2 concentrations reported from Mauna Loa; and (ii) to determine whether differences between these observed (field) and expected (Mauna Loa) levels of ambient carbon dioxide were sufficient to alter plant growth.

Materials and methods

Ambient sampling of atmospheric CO_2

Diurnal values of ambient carbon dioxide concentration [CO_2] were obtained from 4 sites: (i) University of Florida, Gainesville, FL, USA (part of a long-term USDA/University of Florida, SPAR (Soil–Plant–Atmosphere–Research) system to assess the impact of CO_2/temperature on rice production); (ii) University of Western Sydney, Hawkesbury, Richmond, NSW, Australia (part of a greenhouse system to evaluate the impact of CO_2 on C4 plant species); (iii) FACE (Free-Air-CO_2-Enrichment) site, 30 km from Morioka, Japan (from a FACE system designed to assess rising CO_2 on Asian paddy rice); (iv) USDA-ARS, Beltsville, MD, USA (obtained as part of an ongoing study to evaluate rising CO_2 on crop selection and weed/crop interaction using open-top chambers).

Ambient CO_2 was determined at each site (i–iv) as follows: (i) For the SPAR system, ambient CO_2 was determined with a dedicated infrared gas analyser every 2 s and averaged and recorded every 300 s. The ambient sample inlet was 4.4 m above ground level. Moisture was removed from the gas sample by running the line through a refrigerated water trap. The IRGA was calibrated on a weekly basis using pure N_2 and a span gas of 950 µatm. In order to verify linearity of the CO_2 IRGA, standard gases of 351, 750 and 981 µatm were used. (ii) For the Australia data, air inside the ambient glasshouse was sampled with a Fuji Electrics (Japan) IRGA. The voltage output from the IRGA was logged every 15 min by a PC and converted into a µatm reading using a bespoke data acquisition program. The IRGA was calibrated weekly with pure N_2 and a CO_2 calibration gas (352 + 7µatm) (BOC gases, Australia). The output voltage/µatm CO_2 relationship of the IRGA used is linear up to 1000 µatm. (iii) For the Morioka site, ambient air was sampled at plant height from two control plots, one at the northern and the other at the southern end of the experimental field. Because of the prevailing wind direction, either of the two locations is rarely contaminated by elevated CO_2 from the FACE system. In all cases the smaller value of the two recordings was taken as ambient CO_2. CO_2 was sampled using a Li-Cor 6252 in conjunction with a PC/datalogger (Campbell CR10x, Utah). Calibration was performed every other week using a zero and span gas. The sampling interval was 1 s, with one minute averages recorded every 6 min. (iv) for the Beltsville data, CO_2 samples at plant height from a plexi-glass open-top ambient chamber were obtained at 5-min intervals with CO_2 values determined with an CO_2 analyser (Li-Cor. 6252) configured in the absolute mode. For this location, the analyser was calibrated at the beginning of each experiment. For all data sites, ambient diurnal values were determined by averaging the number of data points for a given time period within a 24-h daily cycle over the number of days that experiment was run (e.g. all values
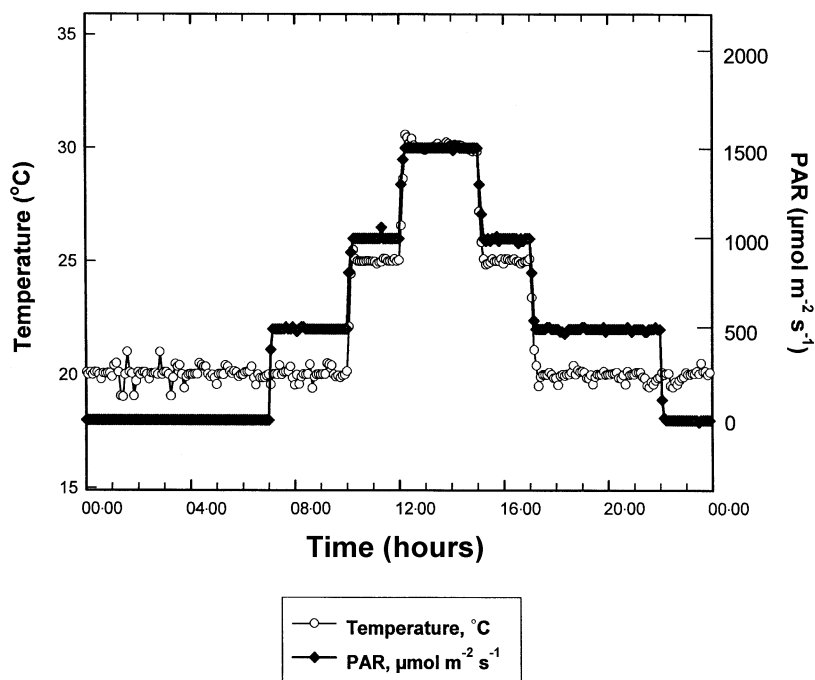
Fig. 1 24-h simulations of temperature (°C) and light (PAR, μmol m^{-1} s^{-1}) for environmental growth chambers under different CO$_2$ concentrations. See methods for additional details.

over the time period 08.00–08.10 hours from 1 June to 1 September).

Comparison of ambient CO$_2$ levels.

In order to simulate different diurnal patterns of ambient CO$_2$, three C3 species – velvetleaf (*Albutilon theophrasti*, L.), tomato (*Lycopersicon esculentum* L., cv. Rutgers) and soybean [*Glycine max*, L. (Merr.), cv Clark] – were grown in three controlled environment chambers (EGC Corp., Chagrin Falls, OH, USA). Two to three seeds of each species were sown in 0.6-L pots filled with vermiculite and thinned to one seedling 2–3 days after emergence. For each treatment 24–26 pots of a given species were used. Pots were arranged to avoid shading from other plants. All pots were watered to the drip point daily with a complete nutrient solution containing 13.5 mmol m^{-3} N (Robinson 1984). Seed for velvetleaf was obtained locally.

For all chambers, temperature was altered in a diurnal fashion (Fig. 1). Light (photosynthetically active radiation, PAR) was supplied by a mixture of high-pressure sodium and metal halide lamps. The CO$_2$ concentration of the air was controlled by adding either CO$_2$ or CO$_2$-free air to maintain the desired CO$_2$ concentration. Injection of CO$_2$ and CO$_2$-free air was controlled by a TC-2 controller using input from an absolute infrared gas analyser (WMA-2, PP Systems, Haverhill, MA, USA). Experiments were performed using three CO$_2$ simulations (Fig. 2): (I) constant day and night CO$_2$ (24-h

average of 377 $\pm$ 1.8 μatm); (II) a build-up of ambient CO$_2$ from 22.00 to 23.00 hours to 500 μatm decreasing to 370 μatm by 06.30 hours (24 h average of 425 $\pm$ 1.4 μatm); (III) same as (II) except CO$_2$ remained elevated at 500 μatm until 09.00 hours then gradually decreasing to 370 μatm by 10.00 hours (24 h average of 437 $\pm$ 2.3). Temperature, light and [CO$_2$] were recorded every 15 min, and averaged for a given experiment.

Plants were grown for 29 days after sowing (DAS). Harvests of six plants were made at 11, 18, 25 and 29 DAS. No visual signs of root-binding were observed in the study. For harvests at 25 and 29 DAS, leaf area was determined photometrically using a leaf area meter (Li-3000; Li-COR Corp., Lincoln, NE, USA). Dry mass was measured separately for leaves, stems and roots after drying at 55 °C for a minimum of 48 h or until dry mass was constant. Relative growth rates (RGR) and net assimilation rates (NAR) were calculated form 25–29 DAS (Jones 1983).

Because only three chambers were available, a randomized complete block design was used with runs over time as replications (blocks). Each chamber was assigned one of the three CO$_2$ treatments. At the end of a given run (i.e. at 29 DAS), CO$_2$ treatments were switched between chambers and the experiment repeated. The entire experiment was repeated three times and pooled data from all three runs are presented. Leaf area and dry mass were analysed for each species using a one-way analysis of variance (ANOVA) with means separated by a least-squares means table. Unless otherwise stated,
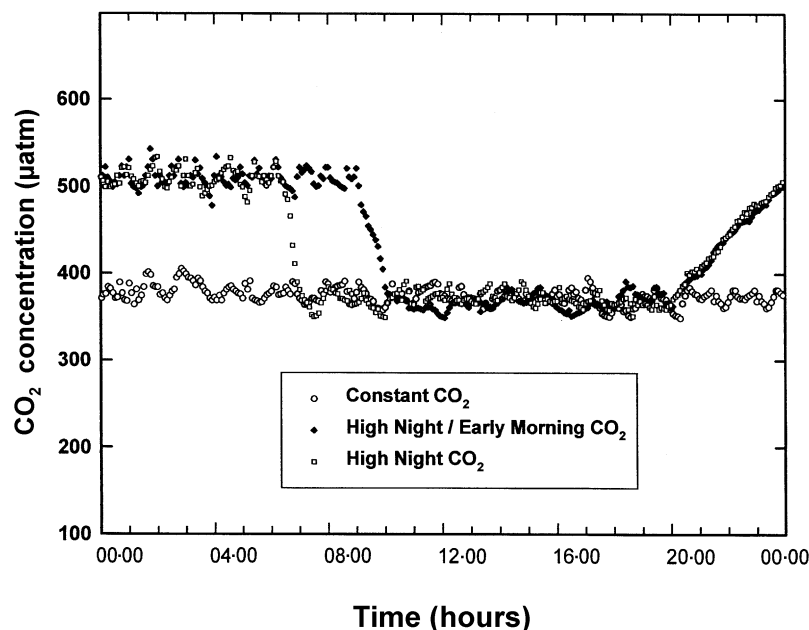
Fig. 2 Simulation of three different diurnal CO_2 patterns: (a) constant day and night CO_2 (24-h average of 377 ± 1.8 µatm, ○); (b) a build-up of ambient CO_2 from 22.00 to 23.00 hours to 500 µatm decreasing to 370 µatm by 06.30 hours (24-h average of 425 ± 1.4 µatm, ◆); (c) same as (b) except CO_2 remained elevated at 500 µatm until 09.00 hours then gradually decreasing to 370 µatm by 10.00 hours (24-h average of 437 ± 2.3, □).

differences between CO_2 treatments were determined as significant at the $P < 0.05$ level.

Results

Ambient CO_2 data from all 4 field sites represent a range of micrometeorological conditions, crop types and experimental techniques. However, all sites show a similar 24-h diurnal pattern of CO_2 concentration with maximum CO_2 observed during the pre-dawn period (03.00–06.00 hours), which decreases to 350–400 µatm CO_2 by mid-morning (08.00–10.00 hours), increasing again by late afternoon/evening (16.00–20.00 hours) (Fig. 3a–d). While showing a similar pattern, absolute values of CO_2 did vary from site to site, with the highest values observed for Richmond, Australia, and Beltsville, USA, sites located within 30 km of large urban centres (Sydney, Australia and Washington, DC, respectively). Overall, 24-h ambient CO_2 averages ranged from a low of 391 ± 36 µatm at Morioka to 466 ± 44 µatm at Richmond. A constant 360 µatm line is shown at all sites for comparison (Fig. 3).

Comparisons of constant 24-h CO_2 (370 µatm) with high night-time carbon dioxide only, indicated no differences in RGR for either tomato or velvetleaf (Fig. 4), although a significant increase in dry biomass and RGR was observed for soybean by 29 DAS (Fig. 4). In contrast, if constant 24-h CO_2 is compared to elevated night-time CO_2, where the higher CO_2 concentration declines during the early morning (i.e. the diurnal simulation of the observed field values), then significant increases in plant biomass are observed for soybean at 25

and 29 DAS and for velveltleaf at 29 DAS (Fig. 5). In addition, significant increases in RGR are observed for all three species from 25 to 29 DAS (Fig. 5).

For specific vegetative characteristics, soybean showed significant increases in leaf area, leaf weight, stem weight for high night-time only CO_2 relative to a constant 24-h CO_2 concentration by 29 DAS (Table 1). Significant increases in leaf area and leaf weight were noted by 29 DAS for both soybean and velveltleaf grown at high night-time/early morning CO_2 relative to the constant 24-h CO_2 concentration. Although absolute values of NAR did vary among species, significant increases in NAR were observed for all species grown at high night-time/early morning CO_2 relative to the constant 24-h CO_2 concentration (Table 1). A significant increase in NAR was also observed for the high night-time only CO_2 relative to a constant 24-h CO_2 concentration in soybean.

Discussion

Within the past 40 years it has been recognized that anthropogenic change associated with fossil fuel burning and deforestation has resulted in increasing atmospheric CO_2, with the observed degree of change sufficient to alter plant photosynthesis and growth (e.g. Lemon 1983). Hundreds of experiments have been conducted to determine the potential responses of individual plant species to rising CO_2. For most of these experiments, future elevated CO_2 is assumed to be double that of the current, ambient CO_2 concentration (cf Poorter 1993). However, because of the constantly rising amount of CO_2 in the air, ambient control levels of CO_2 in plant biology
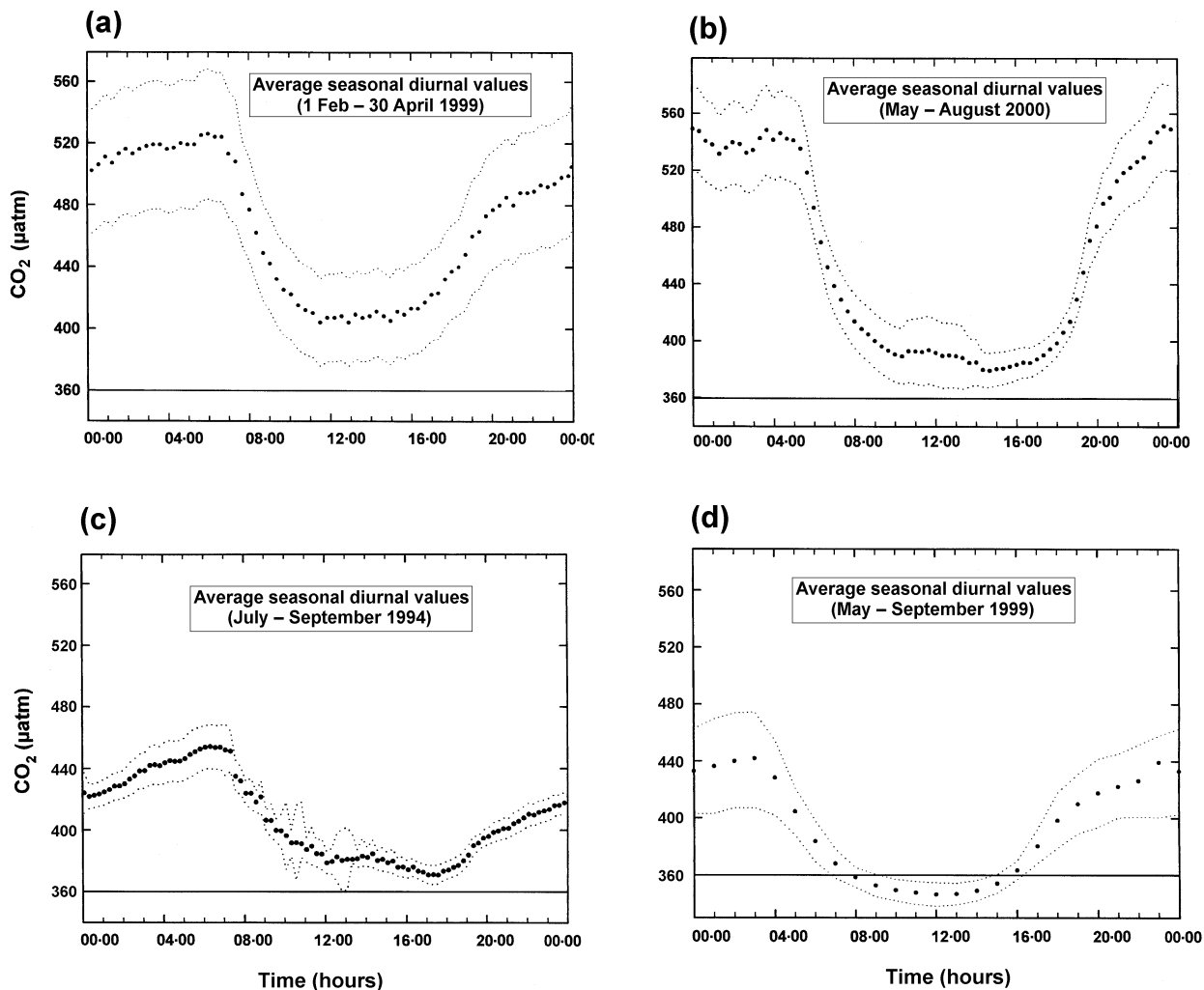
Fig. 3 Average 24-h diurnal CO_2 values for ambient air at four field sites. (a) Greenhouses at University of Western Sydney, NSW, Australia; (b) Open-top chambers at USDA-ARS South Farm, Beltsville, MD, USA; (c) SPAR units at University of Florida, Gainesville, FL, USA; (d) Morioka FACE site, Morioka, Japan. Dashed lines indicate ± 2 SEs. Solid line in each figure represents a constant CO_2 value of 360 µatm. Average 24-h CO_2 values ± SD were 468 ± 44, 458 ± 68, 408 ± 26 and 391 ± 36 µatm, respectively, for each site.

experiments have ranged anywhere from 310 to 360 µatm over the past 30–40 years (see meta-analyses of Kimball *et al.* 1993; Poorter 1993; Curtis & Wang 1998).

For the majority of these experiments, the current level of atmospheric carbon dioxide has been linked to the CO_2 concentration obtained from the Mauna Loa observatory. The data obtained from Mauna Loa is part of the carbon dioxide information analysis centres (CDIAC) effort to monitor global atmospheric CO_2 concentration (Conway *et al.* 1994). The sites associated with the CDIAC are situated in remote locations, usually at higher elevations or along the coast in order to determine CO_2 concentration from large, uncontaminated air masses.

But do these sites accurately reflect the CO_2 concentration encountered by most plants? There are obvious differences related to the amount of industrialization, wind speed, dark respiration, etc., which could influence both the average daily CO_2 encountered as well as the diurnal pattern of CO_2. Average 24-h values of CO_2 for the four field-based sites presented in the current study did vary (468, 458, 408, and 391 µatm for sites in Australia, Maryland, Florida and Japan, respectively), but all sites show a larger 24-h average than that represented by Mauna Loa (i.e. ~360 µatm) and other CDIAC sites. In addition, the ground-based data indicate a substantial shift in the diurnal pattern of CO_2, with significantly higher night-time CO_2 concentrations (exceeding 500 µatm for the Australia and Maryland sites).

Are the differences in CO_2 concentration between ground-based sampling and the long-term Mauna Loa average sufficient to alter the response of plants used as
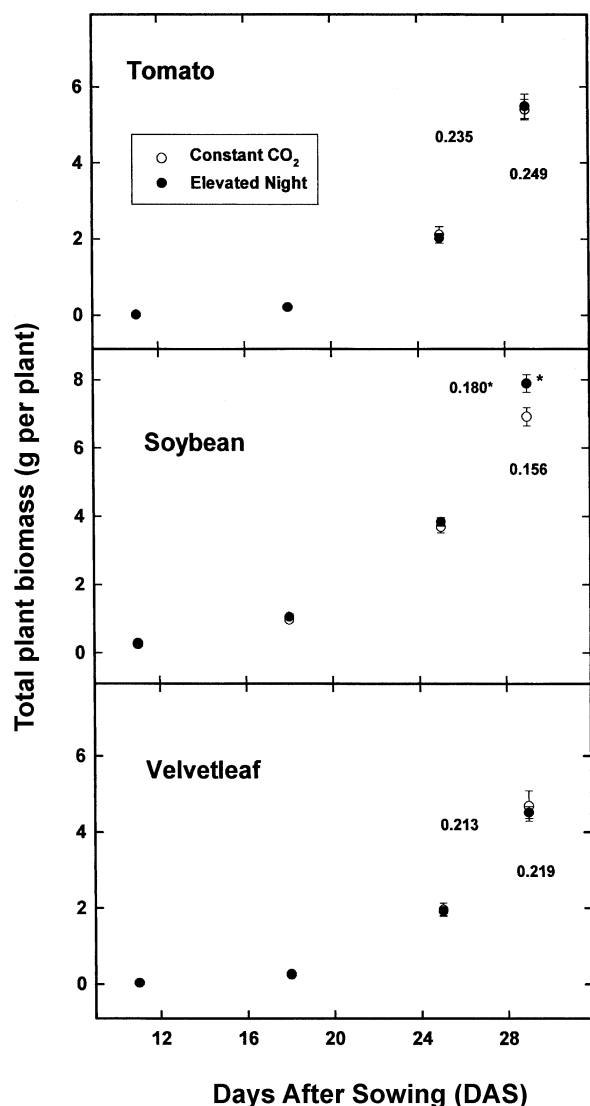
Fig. 4 Total plant biomass at 11, 18, 25 and 29 days after sowing (DAS) for tomato, soybean and velvetleaf grown at either constant CO_2 (370 μatm) or high night-time only (500 μatm) CO_2. An asterisk (*) indicates significant differences in plant biomass for a given sampling time. Numbers indicate RGRs between 25 and 29 DAS for each species; significant differences in RGR are indicated by an asterisk (*).

Fig. 5 Same as Fig. 2, but with high night-time CO_2 extended through until 09.00 horus, then reduced to 370 by 10.00 hours. Morning PAR values were ≈ 500 μmol m^{-2} s^{-1}.

the 'control' in elevated CO_2 experiments? For most of the daylight hours for example, the difference in CO_2 concentration between field based measurements and the long-term Mauna Loa average are relatively small (~10%).

Yet, it is clear in the current data that high CO_2 given only at night can significantly alter dry mass accumulation for soybean. Several studies have shown that high night-time CO_2 can inhibit dark respiration and alter biomass accumulation (Wullschleger *et al.* 1994 and Drake *et al.* 1999; but see also Reuveni *et al.* 1997). For
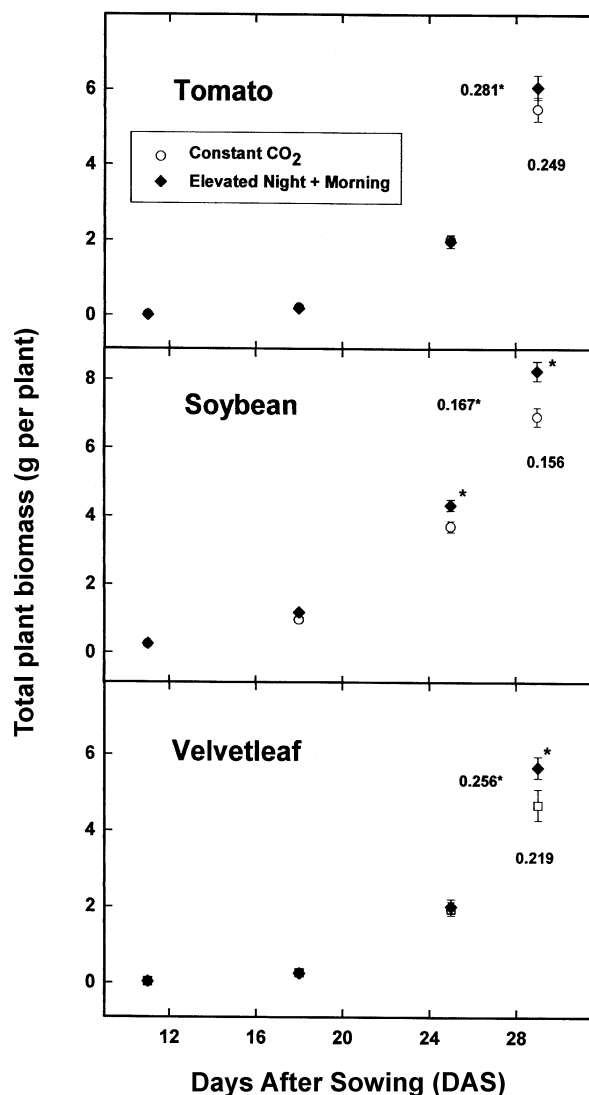
the current study, the stimulation of growth for soybean at high night-time CO_2 only is consistent with that observed for alfalfa and for previous work with soybean (Reuveni & Gale 1985; Bunce 1995). A recent study with red oak has also shown that constant growth at day/night concentrations of 720 μatm CO_2 can accumulate up to 40% greater biomass than red oak grown at day/night concentrations of 720/360 μatm CO_2 (Bunce, unpubl. data), suggesting the importance of high night-time CO_2 with respect to biomass. Inhibition of dark respiration at elevated CO_2 has, in fact, been observed for a number of species (Poorter *et al.* 1992; Amthor 1997); consequently, at least for some species, a constant CO_2 value may

Table 1 Vegetative characteristics and net assimilation rate (NAR) of three C3 species (Velvetleaf, Tomato and Soybean) grown at either constant 370 µatm CO_2, high night-time CO_2 (500 µatm from 20.00 to 07.00 hours) or an approximation of *in situ* CO_2 (build-up of CO_2 to 500 µatm at midnight, 500 µatm CO_2 until 09.00 dissipating to ambient by 10.00 hours. *indicates a significant increase relative to the constant ambient CO_2 control for a given species ($P < 0.05$, assuming unequal variances). Data are from final harvest at 29 days after sowing (DAS)

Species	CO_2	Leaf area (cm^2)	Weight (g $plant^{-1}$) Leaf	Stem	Root	NAR (mg cm^{-2} d^{-1}
Tomato	370 Const.	689	3.76	0.70	1.04	2.00
	500 Night	624	3.70	0.64	0.95	2.00
	500 Morning/Night	734	4.14	0.76	1.17	2.32*
Soybean	370 Const.	940	3.51	1.41	1.99	1.15
	500 Night	1100*	4.11*	1.74*	2.04	1.29*
	500 Morning/Night	1142*	4.14*	1.96*	2.17	1.26*
Velvetleaf	370 Const.	592	2.38	1.12	1.18	1.73
	500 Night	620	2.52	1.05	0.93	1.55
	500 Morning/Night	720*	3.04*	1.26	1.36	2.01*

inadequately describe plant growth for *in situ* CO_2 conditions.

In addition, high night-time CO_2 for all of the field-based sites did not end immediately upon sunrise, but continued through the early morning period diminishing to a constant value by 08.00–10.00 hours. For the present study, growth chamber simulations which extended the high night-time CO_2 period even for a few hours at low light resulted in significant increases in growth, biomass and leaf area for both soybean and velvetleaf, and significant increases in NAR for soybean, velvetleaf and tomato relative to a constant CO_2 value obtained from the long-term Mauna Loa average. It can be argued that additional differences could have been observed at sampling times beyond 29 DAS; however, in general, higher CO_2 levels affect plant growth rates usually during the first 30 days after emergence (Stitt 1991; Ziska & Bunce 1995). Overall, higher CO_2 concentrations even during the morning hours appear to have significant effects on plant growth relative to a constant, fixed CO_2 value.

It is also worth pointing out that the methods used to establish 'ambient' CO_2 conditions do vary. For example, for growth chambers, greater control of ambient CO_2 (and hence a more constant CO_2 value) is achieved relative to glasshouses, SPAR units or FACE systems which generally do not scrub ambient CO_2, particularly at night (e.g. Baker *et al*. 2000). However, within the literature, little distinction is made between high and daytime CO_2 values, and a constant CO_2 concentration is sometimes assumed (e.g. Poorter *et al*. 1992). In addition, treatment conditions of elevated CO_2 have been reported as both ambient $+ x$ µatm, and as a constant higher CO_2 value (e.g. Kimball *et al*. 1993). Given the diurnal, *in situ*

pattern of CO_2 observed here, an elevated CO_2 condition which adds a known amount of CO_2 to an existing ambient would more closely simulate a future, higher CO_2 condition.

One of the obvious advantages to the Mauna Loa data is that they can serve as a global average independent of variations in ground-based CO_2. However, the present study suggests that these variations may be commonly observed by plants in the field and may in themselves have a significant impact on plant biology. As a consequence, what researchers choose as their control and elevated CO_2 values, for plant studies attempting to understand the response of plants to future atmospheric CO_2 conditions, should reflect more realistic *in situ* conditions. Such values would provide a more meaningful assessment of how future CO_2 will impact plant biology. In addition, these values, if properly chosen, can also provide a realistic seasonal assessment of CO_2 variation between suburban (e.g. Australia) and rural (e.g. Japan) areas. Overall, while the present results emphasize the temporal and spatial variations in CO_2 concentration, such variation will provide unique opportunities for researchers to determine whether CO_2 concentration is already a selection factor for ecological fitness under present conditions as well as in a future, higher CO_2 world.

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